
Population Genetics and Structure of Buryats from the Lake Baikal Region of Siberia

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Abstract Genetic polymorphisms of blood groups, serum proteins, red cell enzymes, PTC tasting, and cerumen types are reported for five Mongoloid populations of Buryats from the Lake Baikal region of Siberia (Russia). These groups are characterized by relatively high frequencies of alleles *ABO*B*, *RH*D*, cerumen *D*, *GC*IF*, *ACPI*B*, *ESD*2*, and *PGD*C*. Significant genetic heterogeneity between populations was demonstrated for the loci RH, MN, cerumen, PGD, ABO, GC, GLO, TF, and PGM1. Genetic distance analyses using five loci revealed a lower level of genetic microdifferentiation within the Buryat populations compared with other native Siberian groups. The distribution of gene markers in Buryats is similar to that found in neighboring Central Asian groups, such as the Yakuts and the Mongols. Intrapopulation analyses of the five Buryat subdivisions, based on *R* matrix and r_{ii} , indicate that one of the subdivisions is reproductively more isolated than the others and that two of the communities have received considerable gene flow. A nonlinear relationship was demonstrated between geographic and genetic distances of Buryat population subdivisions.

To date, there is a paucity of information on the distribution of genetic markers in the aboriginal populations of Siberia. The Buryats, one of the largest Asian populations of Russia, inhabit the regions proximal to Lake Baikal. Linguistically, the Buryats are closely related to the Mongols, who speak a language belonging to the Turkish subdivision of the Altaic linguistic family (Hughes 1962). According to Alexseeva et al. (1970), the Buryats anthropologically resemble a number of native Mongoloid groups that settled in an area from northern Central Asia to east of the Ob River and including northern China and Mongolia.

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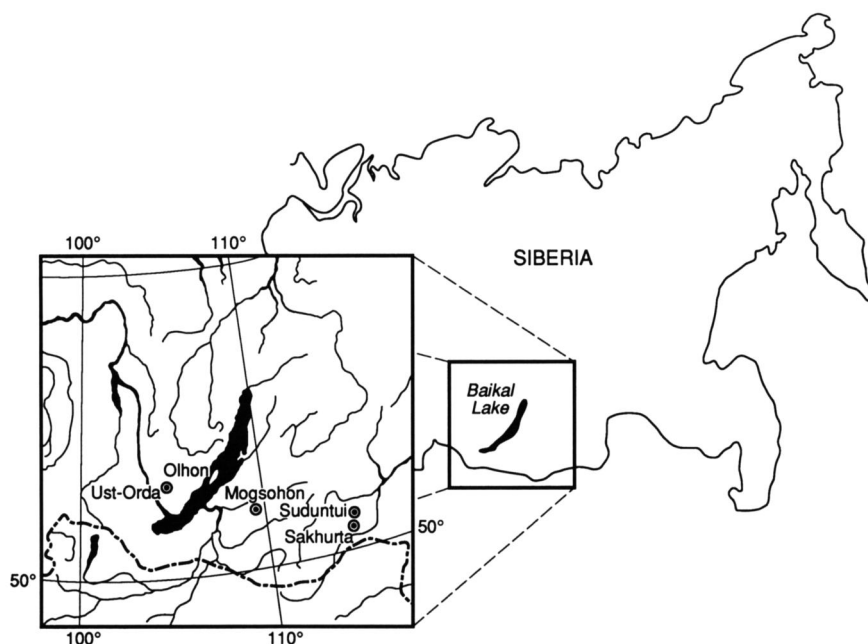


Figure 1. Localization of the Buryat populations.

In this article we present data on the genetic polymorphisms of five geographically separated Buryat populations residing in the vicinity of Lake Baikal. The gene frequencies of these genetic markers are used to reconstruct the structure of the subdivided Buryat population, particularly with respect to the relative roles of systematic and nonsystematic evolutionary pressures in their genetic microdifferentiation.

Materials and Methods

Blood samples were collected from Buryat settlements of the Chita region (Suduntui and Sakhurta settlements), the Irkutsk region (Ust-Orda and Olhon Island on Lake Baikal), and the Kizhinga District (Mogsohon). Figure 1 places these five communities geographically.

The populations were sampled randomly. Both males and females between the ages of 18 and 85 years were included. Serum samples and blood clots were immediately frozen and stored in that condition until phenotyping at the National Research Center of Medical Genetics in Moscow. The ABO, MN, and RH(D) blood groups were typed using standard serological methods [see Alexseeva et al. (1972), Batsuur (1979),

and Batsuur et al. (1991)]. Anti-sera for the ABO and RH systems were obtained from the Moscow City Blood Transfusion Center; MN anti-sera were provided by the Blood Transfusion Institute of St. Petersburg, Russia. Cerumen types were scored into wet or dry categories by inspection. Phenylthiocarbamide (PTC) sensitivity to a concentrated solution was tested during the collection of blood specimens.

The red cell enzymes acid phosphatase (ACP1), esterase D (ESD), and adenylate kinase (AK1) were phenotyped by horizontal starch gel electrophoresis, following the methods of Harris and Hopkinson (1976) with some modifications. Tris-maleine-EDTA buffer (pH 7.2) was used in a horizontal gel, 35–40 V/cm at 4°C for 100–120 min. A specially designed semi-microelectrophoresis starch gel box with a cooling jacket was used to load 40 specimens per run.

The red cell enzyme 6-phosphogluconate dehydrogenase (PGD) was typed using vertical polyacrylamide gels with TEB (tris-EDTA-boric acid) buffer (pH 8.6) (Peacock et al. 1965). Phosphoglucomutase-1 (PGM1) enzyme was phenotyped using isoelectric focusing on polyacrylamide gels following the method of Goedde et al. (1981).

Haptoglobin variation was studied using a starch gel electrophoretic procedure described by Spitsyn (1985).

Alpha-1-antitrypsin (PI), transferrin (TF), and group-specific component (GC) were characterized by isoelectric focusing on agarose gels using the methods of Righetti (1983) and Spitsyn and Titenko (1990).

Analytical Procedures. The blood genetic frequency data were analyzed using several different approaches. Genetic distances for native Siberian populations were computed by using Nei's (1972) method, which was also used to construct a dendrogram. A topographic display of the population affinities was generated by applying the Harpending and Jenkins (1973) method. The relative roles of systematic versus nonsystematic evolutionary pressures on subdivided populations were explored by the Harpending and Ward (1982) method, which predicts the existence of a linear relationship between heterozygosity in a subgroup and its distance from the centroid of distribution. Extreme deviation from this expected relationship is indicative of the possible action of systematic or nonsystematic evolutionary pressures.

To measure the probable relationship between the genetic similarity of the subgroups and geography, we computed a product-moment correlation between the elements of the genetic distance matrix ($d_{ij}^2 = r_{ii} + r_{ij} - 2r_{ij}$) and of the straight-line geographic distance matrix (Harpending and Jenkins 1973). The significance of this correlation is tested through the Mantel matrix permutation procedure (Relethford 1990). Because our analysis consisted of five populations, all possible permutations were used, which is $5! = 120$.

Results and Discussion

Phenotypic and allelic frequencies in the Buryat populations are listed in Table 1. Chi-square tests for Hardy-Weinberg equilibrium have revealed some isolated cases of disequilibrium at low levels of significance in the Suduntui, Olhon, and Mogsohon populations (see Table 2).

Several cases of disequilibrium in the Ust-Orda population exhibit an excess of heterozygotes MN and TF C1,C2 and an excess of homozygotes PGM1 2A,2A (see Table 2). No age or sex trends were observed in the distribution of MN, TF, and PGM1 polymorphisms when different age and sex cohorts from Ust-Orda were compared (data not shown). These negative findings complicate the interpretation of the possible population structure mechanisms responsible for the observed disequilibria. It is for this reason that we regressed mean per locus heterozygosity on the distance from the centroid of distribution; we found that Ust-Orda has medium levels of heterozygosity but low r_{ii} . These results suggest considerable gene flow and present little evidence of the action of stochastic processes (see Figure 5).

The tests for the genetic homogeneity of the five Buryat populations are shown in Table 3. Significant heterogeneity (at $p < 0.05$ level) among the five Buryat groups is demonstrated for the loci RH, MN, cerumen, PGD, ABO, GC, GLO1, TF, and PGM1. These differences by locus between the subdivisions are due to varying degrees of recent genetic admixture, a founder effect in the original subdivision, or genetic microdifferentiation. A previous physical anthropological study of Buryats by Alexseeva et al. (1970) also observed considerable genetic heterogeneity among other subdivided populations.

Compared with other indigenous populations of Siberia, the Buryats have relatively high frequencies of the alleles *ABO*B*, *RH*D*, cerumen *D*, *GC*IF*, *ACP*B*, *ESD*2*, and *PGD*C*. In the populations of the Chita region (Suduntui and Sakhurta), the *PGD*C* allele has, to date, the highest frequency observed in any native Siberian population.

Because most of the genetic marker studies of native Siberian populations were published in Russian, a comparison of the allelic frequency distributions among the Buryat villages and with other ethnic groups may be useful (Alexseeva et al. 1972; Batsuur et al. 1985, 1991; Boeva 1988; Emialanova et al. 1976). Historically, the people of Siberia, as a result of relative geographic isolation, evolved separately into three Asian linguistic groups: Samoyedic (Uralic-Western), Tungusic (North Asian-Central), and Paleo-Asiatic speakers (Northeastern). In addition, there are a number of groups that speak unique languages (such as the Kets and Ngansan) whose linguistic affiliation has perplexed linguists. The genetic variability within the indigenous Siberian population is high, and it is difficult to discern any particular pattern within any of the three

Table 1. Phenotype and Allele Frequencies of Polymorphic Genes in Buryat Populations

System, Phenotype, Allele	Frequency				
	<i>Suduntui</i>	<i>Sakhurta</i>	<i>Ust-Orda</i>	<i>Olhon</i>	<i>Mogsohon</i>
ABO					
Phenotype					
ABO O	117	55	156	34	75
ABO A	57	33	129	18	80
ABO B	106	37	185	32	46
ABO AB	15	9	49	6	12
Total	295	134	519	90	213
Allele					
<i>ABO*O</i>	0.624	0.642	0.546	0.613	0.565
<i>ABO*A</i>	0.138	0.170	0.193	0.145	0.150
<i>ABO*B</i>	0.239	0.188	0.262	0.242	0.284
MN					
Phenotype					
M	110	50	114	30	
MN	151	61	319	46	
N	34	22	83	14	
Total	295	133	516	90	
Allele					
<i>M</i>	0.629	0.605	0.530	0.589	
<i>N</i>	0.371	0.395	0.470	0.411	
RH					
Phenotype					
D+	288	133	516	86	289
D-	6	1	3	4	0
Total	294	134	519	90	289
Allele					
<i>RH*D</i>	0.857	0.914	0.924	0.789	1.000
PTC					
Phenotype					
PTC+	229	98	409	71	232
PTC-	57	21	108	19	50
Total	286	119	517	90	289
Allele					
<i>T</i>	0.554	0.580	0.543	0.541	0.556
<i>NT</i>	0.446	0.420	0.457	0.459	0.444
Ear wax (cerumen)					
Phenotype					
Wet	49	11	1	12	50
Dry	217	89	424	78	218
Total	266	100	425	90	268
Allele					
<i>W</i>	0.097	0.057	0.001	0.069	0.098
<i>D</i>	0.903	0.943	0.999	0.931	0.902

Table 1. Continued

<i>System, Phenotype, Allele</i>	<i>Frequency</i>				
	<i>Suduntui</i>	<i>Sakhurta</i>	<i>Ust-Orda</i>	<i>Olhon</i>	<i>Mogsohon</i>
HP					
Phenotype					
HP 1	23	16	47	7	15
HP 1,2	139	67	34	34	128
HP 2	128	51	237	44	144
Total	290	134	488	85	287
Allele					
<i>HP*1</i>	0.319	0.305	0.305	0.282	0.275
<i>HP*2</i>	0.681	0.695	0.718	0.718	0.725
GC					
Phenotype					
GC 1F			123	27	65
GC 1F,1S } 1	177	70	132	25	72
GC 1S } }			60	7	24
GC 1F,2 } 1,2			88	12	62
GC 1S,2 } }	102	56	68	12	46
GC 2			18	2	16
Total	290	134	489	85	285
Allele					
<i>GC*1</i>	0.786	0.731			
<i>GC*1F</i>			0.477	0.535	0.463
<i>GC*1S</i>			0.327	0.300	0.291
<i>GC*2</i>	0.296	0.269	0.196	0.165	0.246
TF					
Phenotype					
TF C1	186	81	288	47	158
TF C1,C2	87	35	175	35	99
TF C1,C3	2	1	2	0	0
TF C1,B	0	1	5	1	0
TF C1,D	8	6	6	0	5
TF C2	8	8	8	2	19
TF C3	1	0	0	0	0
TF C2,C3	0	1	0	0	0
TF C2,B	0	0	1	0	0
TF C2,D	2	1	1	0	3
TF C3,D	1	0	0	0	0
Total	295	134	486	84	285
Allele					
<i>TF*C1</i>	0.795	0.765	0.784	0.768	0.739
<i>TF*C2</i>	0.178	0.198	0.198	0.232	0.246
<i>TF*C3</i>	0.009	0.008	0.002		
<i>TF*B</i>		0.004	0.008	0.002	
<i>TF*D</i>	0.019	0.026	0.007		0.014

Table 1. Continued

<i>System, Phenotype, Allele</i>	<i>Frequency</i>				
	<i>Suduntui</i>	<i>Sakhurta</i>	<i>Ust-Orda</i>	<i>Olhon</i>	<i>Mogsohon</i>
PI					
Phenotype					
PI M1	182	97	287	45	171
PI M1,M2	58	21	106	21	69
PI M1,M3	37	9	36	7	28
PI M1,S	0	0	0	0	0
PI M1,Z	1	0	1	4	5
PI M2	6	3	13	5	7
PI M3	4	2	3	1	1
PI M2,M3	2	1	5	1	3
PI M2,S	0	0	0	0	1
PI M2,Z	0	0	0	0	1
Total	290	133	451	84	286
Allele					
<i>PI*M1</i>	0.793	0.842	0.795	0.726	0.776
<i>PI*M2</i>	0.124	0.105	0.152	0.191	0.153
<i>PI*M3</i>	0.081	0.053	0.052	0.060	0.058
<i>PI*S</i>					0.002
<i>PI*Z</i>	0.002		0.001	0.024	0.010
ACP1					
Phenotype					
ACP1 A	22	15	45	11	29
ACP1 A,B	113	45	206	27	117
ACP1 A,C	0	0	2	0	0
ACP1 B	157	65	224	47	139
ACP1 B,C	4	4	3	0	0
Total	296	129	480	85	285
Allele					
<i>ACPI*A</i>	0.265	0.289	0.310	0.288	0.307
<i>ACPI*B</i>	0.728	0.689	0.684	0.712	0.693
<i>ACPI*C</i>	0.007	0.023	0.005		
PGM1					
Phenotype					
PGM1 1A	165	60	224	45	128
PGM1 1B	1	0	1	3	4
PGM1 2A	5	2	32	0	9
PGM1 2B	0	0	0	0	1
PGM1 1A,1B	43	29	73	9	35
PGM1 1A,2A	50	31	107	19	75
PGM1 1A,2B	15	3	16	3	18
PGM1 1B,2A	12	6	17	5	12
PGM1 1B,2B	3	0	3	0	0
PGM1 2A,2B	1	0	4	1	1
Total	295	131	477	85	283
Allele					
<i>PGMI*1A</i>	0.724	0.699	0.675	0.712	0.678
<i>PGMI*1B</i>	0.102	0.134	0.100	0.118	0.097
<i>PGMI*2A</i>	0.124	0.157	0.201	0.147	0.187
<i>PGMI*2B</i>	0.032	0.012	0.024	0.024	0.037

Table 1. Continued

<i>System, Phenotype, Allele</i>	<i>Frequency</i>				
	<i>Suduntui</i>	<i>Sakhurta</i>	<i>Ust-Orda</i>	<i>Olhon</i>	<i>Mogsohon</i>
PGD					
Phenotype					
PGD A	214	86	412	75	214
PGD A,C	78	41	65	10	73
PGD C	4	4	4	0	1
Total	296	131	481	85	288
Allele					
PGD*A	0.855	0.813	0.924	0.941	0.870
PGD*C	0.145	0.187	0.076	0.059	0.130
ESD					
Phenotype					
ESD 1	190	80	270	53	180
ESD 1,2	91	46	183	24	89
ESD 2	13	5	27	7	16
Total	294	131	480	84	288
Allele					
ESD*1	0.801	0.786	0.753	0.773	0.788
ESD*2	0.199	0.214	0.247	0.226	0.212
GLO1					
Phenotype					
GLO1 1	15	1	8	5	
GLO1 1,2	68	24	111	25	
GLO1 2	204	106	363	55	
Total	287	131	482	85	
Allele					
GLO*1	0.171	0.099	0.132	0.206	
GLO*2	0.829	0.901	0.868	0.794	
AK					
Phenotype					
AK 1	281	130	476	85	283
AK 1,2	15	2	5	0	3
Total	296	132	481	85	286
Allele					
AK*1	0.975	0.992	0.995	1.000	0.995
AK*2	0.025	0.008	0.005	0	0.005

groups, although there are differences in the presence of specific markers, such as a high frequency of *ACP*A* in Paleo-Asian populations and a high frequency of *PTC*T* in Uralic groups (see Table 4).

Table 5 summarizes the gene frequencies used in the analysis of genetic distances computed by Nei's (1972) method. The allelic frequencies from 5 polymorphic loci [ABO, RH(D), HP, PGM1, and ACP1] were compiled for 14 neighboring Siberian indigenous populations plus

Table 2. Chi-Square Testing of Hardy-Weinberg Equilibrium for Codominant Loci

<i>Locus</i>	<i>Suduntui</i>		<i>Sakhuria</i>		<i>Ust-Orda</i>		<i>Olhon</i>		<i>Mogsohon</i>	
	χ^2	<i>d.f.</i>	χ^2	<i>d.f.</i>	χ^2	<i>d.f.</i>	χ^2	<i>d.f.</i>	χ^2	<i>d.f.</i>
ABO	1.07	1	0.02	1	0.24	1	0.02	1	4.63 ^a	1
MN	2.75	1	0.21	1	29.95 ^b	1	0.28	1		
HP	3.09	1	1.62	1	0.10	1	0.01	1	3.28	1
TF	0.56	1	2.37	1	10.91 ^b	1	0.98	1	0.56	1
PI	4.32 ^a	1	1.02	1	1.42	1	0.59	1	1.10	1
GC	0.62	1	0.54	1	5.76	4	2.67	3	1.43	1
ACP1	0.08	1	2.80	1	0.06	1	4.34 ^a	1	0.35	1
PGM1	3.67	2	2.79	1	15.24 ^b	3	2.54	1	2.69	1
PGD	1.11	1	0.03	1	0.09	1	0.04	1	0.99	1
ESD	0.25	1	0.26	1	0.31	1	2.84	1	1.25	1
AK1	0.20	1	0.08	1	0.01	1			0.01	1

a. Significant disequilibrium, $p < 0.05$.b. $p < 0.01$.

Table 3. Chi-Square Testing of Homogeneity among Five Buryat Groups

<i>Locus</i>	<i>Allele</i>	χ^2	<i>d.f.</i>	<i>p</i>
ABO		19.80	8	<0.05
	<i>O</i>	12.92	4	<0.05
	<i>A</i>	9.57	4	<0.05
	<i>B</i>	8.26	4	NS
MN		16.61	3 ^a	<0.01
RH		117.37	4	<0.001
PTC		1.23	4	NS
Cerumen		83.54	4	<0.001
HP		3.16	4	NS
TF	<i>TF*C1</i>	6.31	4	NS
	<i>TF*C2</i>	9.48	4	<0.05
	<i>TF*C3</i>	8.56	4	NS
	<i>TF*B</i>	8.33	4	NS
PI	<i>PI*M1</i>	9.31	4	NS
	<i>PI*M2</i>	8.96	4	NS
	<i>PI*M3</i>	5.77	4	NS
GC ^b		12.35	4	<0.05
ACP1	<i>ACP1*A</i>	4.10	4	NS
	<i>ACP1*B</i>	3.71	4	NS
PGM1	<i>PGM1*1A</i>	9.01	4	NS
	<i>PGM1*1B</i>	3.31	4	NS
	<i>PGM1*2A</i>	17.57	4	<0.01
	<i>PGM1*2B</i>	5.47	4	NS
PGD		39.91	4	<0.001
ESD		5.63	4	NS
GLO1		13.93	3 ^a	<0.05

a. Sample from Mogsohon has not been tested for the MN and GLO1 polymorphisms.

b. GC electrophoretic types have been considered.

the 5 Buryat villages. The Buryats are compared to such populations as the Mongols and the Yakuts, who belong to the North Asian group of populations. The genetic distance comparison is summarized in Table 6, which presents Nei's distances multiplied by 10^5 . The Buryats of Mogsohon show strong affinities to the Mongols of Mongolia and are particularly close to the Yakuts of Megino-Kangalas. In fact, Mogsohon shows greater affinities to the Yakuts than to any other Buryat subdivision. This suggests Buryat admixture with the Yakuts. The genetic proximity of all the Buryat subdivisions to the Mongols attests to their Mongolian origins.

Figure 2 is a dendrogram based on five loci used to compute Nei's genetic distances. The genetic relationships between the various Siberian indigenous populations are indicated. Cluster R1 on this dendrogram is made up entirely of the North Asian groups of central Siberia. The Sundutui, Sakhurta, and Ohlon Island Buryats form a tight cluster, whereas

Table 4. Variability of Allele Frequencies for Some Gene Markers in Three Main Groups of Siberian Populations

Allele	Group of Populations			References ^a
	Uralic	North Asiatic	Arctic	
<i>ABO*O</i>	0.49–0.79	0.34–0.80	0.38–0.73	1–26
<i>ABO*A</i>	0.08–0.35	0.07–0.36	0.09–0.32	
<i>ABO*B</i>	0.02–0.33	0.01–0.41	0.01–0.35	
<i>MN</i>	0.11–0.70	0.15–0.78	0.29–0.64	4, 6, 7, 9, 11, 16–18, 21, 23, 24, 26–29
<i>RH*D</i>	0.58–1.00	0.79–1.00	1.00	2, 4, 6–8, 10–14, 16–18, 23, 24, 26, 27, 29–32
<i>PTC*T</i>	0.11–0.48	0.49–0.72	0.30–0.71	8, 12, 16, 17, 19–22, 33, 34
Cerumen <i>W</i>	0.34–0.72	0.00–0.21		35–38
<i>HP*1</i>	0.01–0.50	0.18–0.48	0.10–0.50	1–4, 8, 10–14, 16–22, 27, 29, 30, 33, 37, 39–43
<i>TF*CI</i>	0.91–1.00	0.88–1.00	0.97–1.00	2, 7, 10, 11, 16, 17, 21, 29,
<i>TF*B_{S-I}</i>	0.00–0.06	0.00–0.05	0.00	30, 37, 41, 43, 44
<i>TF*D_{Chi}</i>	0.00–0.03	0.00–0.13	0.01–0.03	
<i>GC*1</i>	0.62–0.82	0.52–0.92	0.57–0.91	2, 3, 10, 17, 19–22, 37
<i>P*A</i>	0.06–0.40	0.00–0.49	0.45–0.73	2, 4, 7, 10, 11, 19, 20, 22, 23,
<i>P*B</i>	0.56–0.94	0.51–1.00	0.27–0.55	29, 30, 37, 41, 44
<i>P*C</i>	0.01–0.05	0.00–0.15	0.00–0.01	
<i>PGM1*2</i>	0.13–0.58	0.04–0.37	0.01–0.30	4, 7, 10, 11, 19–23, 29, 30, 37, 41, 44
<i>ESD*2</i>	0.11–0.17	0.01–0.25	0.06–0.22	2, 10, 19–22, 41, 44
<i>GLO*1</i>	0.28–0.51	0.08–0.44	0.08–0.45	10, 19–21, 37, 41, 44
<i>PGD*C</i>	0.02–0.18	0.02–0.19	0.02–0.10	2, 7, 11, 19–22, 29, 30, 37
<i>AK*2</i>	0.00–0.03	0.00–0.04		7, 21, 23, 29, 30

- a. (1) Batsuur (1979); (2) Batsuur et al. (1991); (3) Benevolenskaya et al. (1981); (4) Boeva (1988); (5) Eriksson, Lehmann, and Simpson (1979); (6) Ismagulov (1981); (7) Karaphet et al. (1981); (8) Lemza et al. (1987); (9) Levin (1959); (10) Novoradovsky et al. (1985); (11) Posukh et al. (1990); (12) Puzirev et al. (1985); (13) Rafikov, Belova et al. (1981); (14) Rafikov, Yumaguzhina, and Kuzeev (1981); (15) Rychkov (1965b); (16) Rychkov and Sheremetieva (1972a); (17) Rychkov and Sheremetieva (1972b); (18) Rychkov et al. (1984); (19) Shneider et al. (1990); (20) Solovenchuk and Avanesova (1977); (21) Solovenchuk et al. (1985); (22) Solovenchuk and Glushenko (1985); (23) Spitsyn and Titenko (1990); (24) Tikhomirova (1990); (25) Voronina (1975); (26) Voronina and Tausik (1977); (27) Emelianova et al. (1976); (28) Levin (1958); (29) Sukernik et al. (1977); (30) Sukernik et al. (1978); (31) Sukernik et al. (1980); (32) Sukernik et al. (1979); (33) Alexseeva et al. (1972); (34) Luzina et al. (1976); (35) Eriksson, Zolotareva et al. (1979); (36) Kasenov and Sundetov (1984); (37) Solovenchuk et al. (1984); (38) Spitsyn (1985); (39) Hromova (1975); (40) Kasenov and Sundetov (1985); (41) Rychkov and Sheremetieva (1978); (42) Solovenchuk (1989); (43) Voronina and Zhukova (1975); (44) Sharav (1970).

Table 5. Allele Frequencies of Some Loci in the Native Siberian Populations

<i>Population</i>	<i>ABO*A</i>	<i>ABO*B</i>	<i>RH*D</i>	<i>HP*1</i>	<i>ACPI*A</i>	<i>ACPI*B</i>	<i>PGM1*2</i>	<i>Reference^a</i>
Buryats								
Mogohon	0.150	0.284	1.000	0.275	0.307	0.693	0.224	1
Sakurta	0.170	0.188	0.914	0.310	0.289	0.689	0.168	1
Ust-Orda	0.193	0.262	0.924	0.305	0.310	0.684	0.225	1
Olhon	0.145	0.242	0.789	0.282	0.288	0.712	0.171	1
Suduntui	0.138	0.239	0.857	0.319	0.265	0.728	0.156	1
Chukchi, Coastal	0.201	0.126	1.000	0.310	0.584	0.416	0.116	6, 7
Chulymtsi, Tomsk region	0.095	0.171	1.000	0.153	0.405	0.595	0.194	4
Evens, Yakutia	0.231	0.159	1.000	0.416	0.276	0.724	0.115	5
Mongols, Mongolia	0.168	0.220	0.925	0.273	0.243	0.756	0.209	2
Nenets								
Tarko-Sale	0.194	0.225	0.928	0.380	0.247	0.720	0.407	9
Sytomino	0.231	0.079	1.000	0.484	0.062	0.938	0.125	9
Variogan	0.081	0.130	0.972	0.427	0.233	0.754	0.207	9
Numto Lake	0.217	0.162	0.882	0.382	0.088	0.912	0.235	9
Yamal (pooled data)	0.140	0.230	0.932	0.390	0.190	0.794	0.345	9
Nganasans, Vorontsovo	0.174	0.162	1.000	0.239	0.006	0.994	0.167	8
Yakuts								
Megino-Kangalas District	0.181	0.260	1.000	0.290	0.247	0.743	0.221	3
Ust-Aldan District	0.176	0.228	1.000	0.351	0.200	0.792	0.178	3
Yukagirs, Yakutia	0.360	0.170	1.000	0.390	0.384	0.616	0.080	5

a. (1) This study; (2) Batsuur et al. (1991); (3) Boeva et al. (1988); (4) Novorodovsky et al. (1985); (5) Posukh et al. (1990); (6) Rychkov and Sheremetieva (1972b); (7) Solovenchuk (1984); (8) Sukernik et al. (1978); (9) Sukernik et al. (1980).

Table 6. Genetic Distances of Nei (1972) between Some Native Siberian Populations ($\times 10^{-5}$)

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Buryats, Mogsohon																	
2. Buryats, Sakhurta	617																
3. Buryats, Ust-Orda	208	349															
4. Buryats, Olhon	535	588	854														
5. Buryats, Suduntui	968	206	521	206													
6. Chukchi, Coastal	3319	2853	3286	4493	4028												
7. Chulymtsi, Tomsk region	3116	1407	1740	2385	2175	2060											
8. Evens, Yakutia	1346	733	1129	2169	1150	3285	3191										
9. Mongols, Mongolia	409	238	272	676	333	4240	1618	1193									
10. Nenets, Tarko-Sale	1660	2123	1427	2987	2453	6521	4033	2855	1615								
11. Nenets, Sytomino	4122	2812	3796	4313	2938	8835	6951	1522	2859	4085							
12. Nenets, Variogan	2043	1128	1972	2421	1442	4692	3094	1145	1467	2199	1500						
13. Nenets, Numto Lake	2633	1802	2076	2138	1543	8828	5457	1970	1288	2020	1071	1737					
14. Nenets, Yamal (pooled)	1495	1600	1325	2345	1671	6954	3943	2144	1097	335	2506	1221	985				
15. Nganasan, Vorontsovo	2734	2426	2880	3167	2384	9757	4714	2877	1548	3761	1895	2753	1008	2310			
16. Yakuts, Megino-Kangalas	124	591	256	1547	887	4193	1889	1062	258	1455	3063	1794	1756	1123	1845		
17. Yakuts, Ust-Aldan	620	589	638	1671	780	4809	2751	519	418	1755	1585	1088	1050	1012	1350	266	
18. Yukagirs, Yakutia	2253	1927	1851	3452	2610	2474	4125	953	2664	4751	4394	3952	4602	4726	5764	2201	2118

Loci used: ABO, RH, HP, ACPI, PGM1.

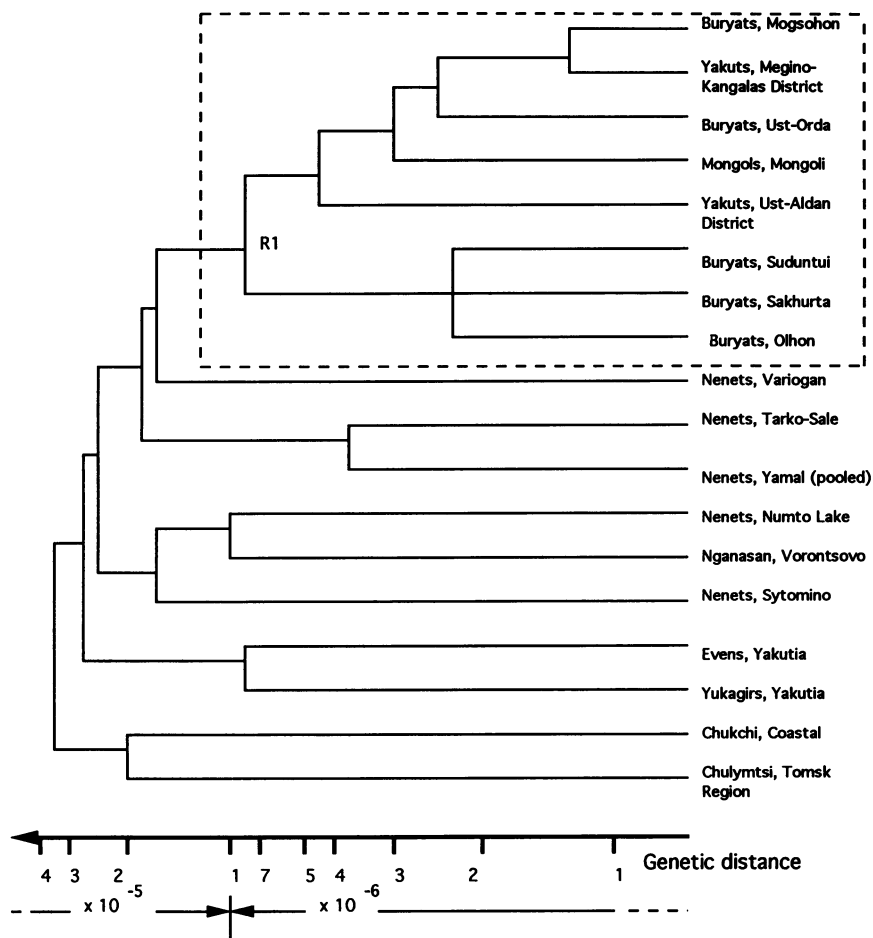


Figure 2. Genetic relationships between 18 Siberian populations graphically presented by a dendrogram based on 5 genetic loci (ABO, RH, HP, ACP1, and PGM1) and Nei's (1972) measure of genetic distances.

the Buryats of Mogsohon show greater affinity to the Yakuts. The position of Mogsohon provides further credence to gene flow from the Yakuts.

An *R* matrix analysis was conducted on the 5 Buryat population subdivisions using frequencies from 11 genetic loci and 27 alleles. Figure 3 depicts the dispersal of the five Buryat villages along the first two scaled eigenvectors. Together these two eigenvectors explain 74.6% of the total variation. The first axis represents 45.9% of the variation, and the second axis explains 30.5%. The first axis exhibits separation of the Chita region Buryat groups (Suduntui and Sakhurta) from the Ust-Orda

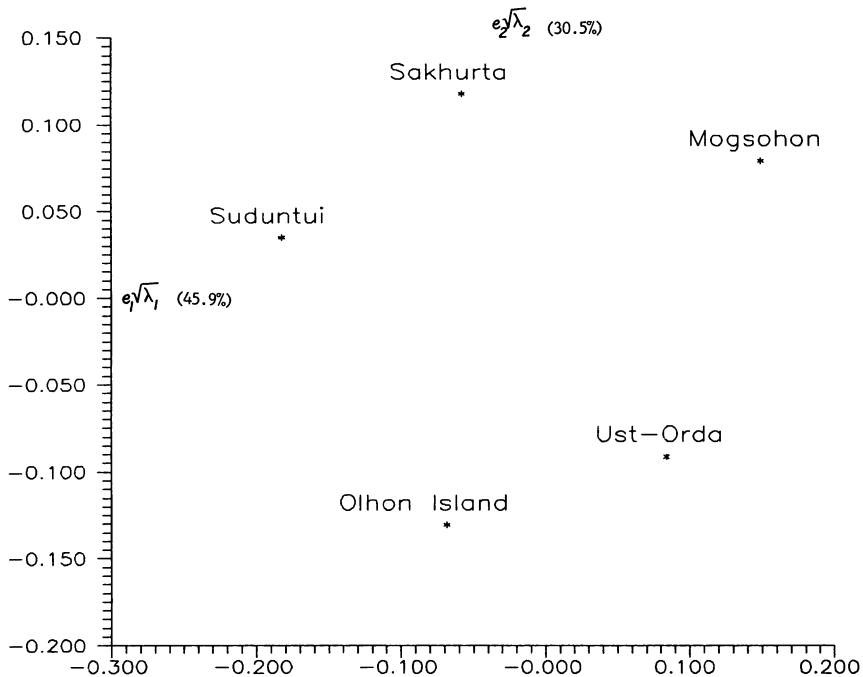


Figure 3. Least-squares reduction genetic map of 5 Buryat groups based on 27 allelic frequencies.

(Irkutsk region) and Mogsohon (Kizhinga district, Buryatia) groups. However, the population of Olhon Island, although from the region of Irkutsk, aligns with the Chita region groups, probably exhibiting the distinctiveness of an island population within the Irkutsk region. Such a relationship can also be understood as a relatively closer genetic affinity of Olhon Island with the Chita region groups. In fact, as is shown in the dendrogram (Figure 2, R1 cluster), the population of Olhon Island joins the two Chita regional groups, forming a tight cluster within the North Asian groups of Central Asia.

The second axis of the R matrix plot clearly separates the groups west of Lake Baikal (i.e., Ust-Orda and Olhon Island) from the populations that inhabit the eastern side of Lake Baikal (i.e., Suduntai, Sakhurta, and Mogsohon). Indeed, such a discrimination corresponds well to the geographic locations of these groups.

Figure 4 is a plot of the distribution of traits that underlie the population separation along the first two eigenvectors shown in Figure 3. The high frequencies of alleles PGD^*C , TF^*D , and GC^*2 in the Chita region groups are responsible for their separation from the other groups.

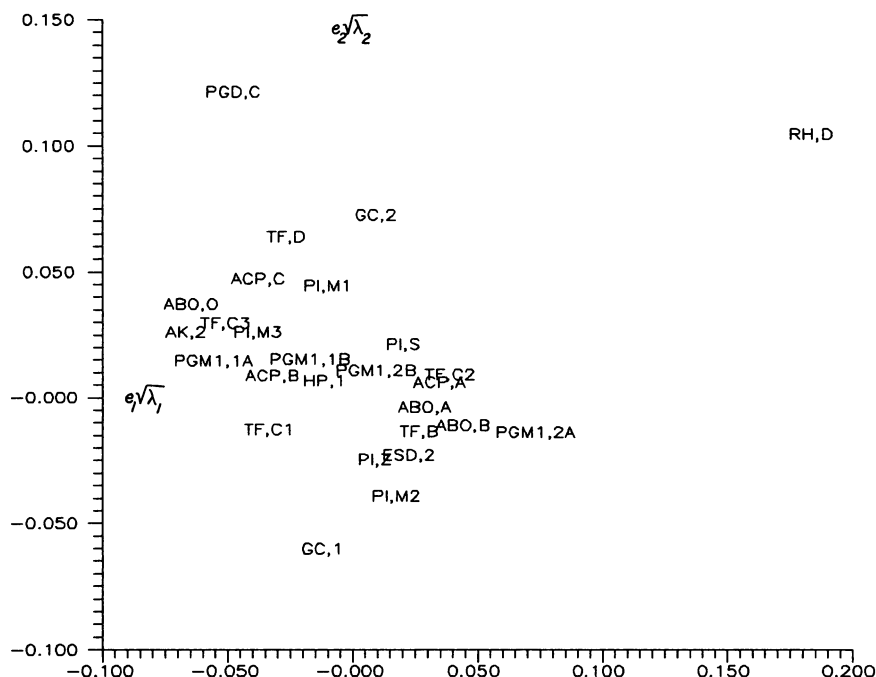


Figure 4. Distribution of alleles along the first and second scaled eigenvectors for five Buryat groups.

As indicated earlier, these two populations have the highest incidence of *PGD*C* among native Siberian groups. The uniqueness of the Ohlon Island population is due to the frequencies of *GC*1* and *PI*M2*. The separation of the populations of Mogsohon and Ust-Orda from the other three groups is primarily due to the high frequencies of *RH*D* and *PGM1*2A*, respectively.

Under the assumption of uniform systematic pressure, Harpending and Ward (1982) predicted the existence of a linear relationship between heterozygosity H in a subgroup and its distance from the centroid of distribution. Such a relationship is expressed as a uniform negative regression with slope $-Hp$ and intercept Hp . The positive and negative departures from the predictions reveal the nature of differential systematic or nonsystematic pressures exerted on related subpopulations. In general, such positive and negative deviations suggest the effects of gene flow and some sort of stochastic process (genetic drift or bottleneck or a founder effect). Given these theoretical underpinnings, Figure 5 can be interpreted in evolutionary terms. The population of Suduntui is more isolated from the other Buryat villages, followed by Ust-Orda and Olhon Island (the last two subdivisions are close to the predicted relationship

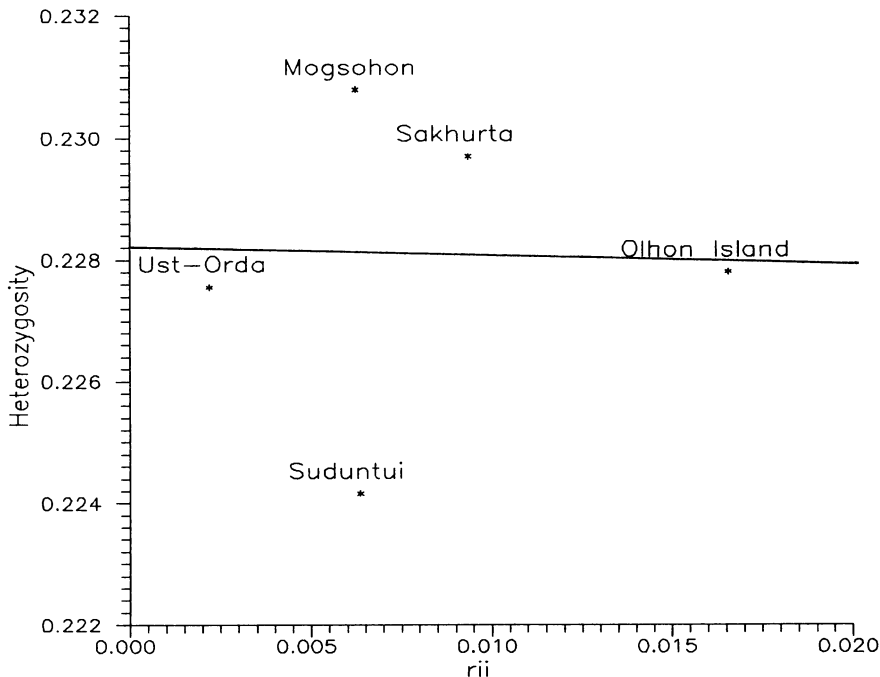


Figure 5. Plot of heterozygosity and distance from the centroid of distribution (r_{ii}) for five Buryat groups.

between heterozygosity and the distance from the centroid). The high levels of heterozygosity in Mogsohon and Sakhurta suggest gene flow into those subdivisions. The Olhon Island subpopulation of Buryats is located on Lake Baikal and is geographically isolated from all the other surrounding communities. This isolation is in fact reflected by the greatest distance from the centroid, but this village also has moderate heterozygosity. Recently, tourism may have contributed to the flow of genes into this subpopulation, and the relative position of Olhon Island in Figure 5 may reflect a genetic isolate experiencing the breakdown of reproductive isolation.

Mantel Correlations. A comparison of the elements of genetic and geographic distance matrices using product-moment correlation reveals a low to moderate association of $r = 0.30$. The $p = 0.15$, tested through the Mantel matrix permutation procedure, is nonsignificant. As noted by Sokal and Rohlf (1981, p. 601), "the product-moment correlation coefficient describes the linear component of the relations between two variables. Depending on the nonlinearity and the range of values used in computing the coefficient, even a strictly deterministic phenomenon may

have a nonsignificant linear correlation." With regard to the product-moment correlation used to measure the possible association between geography and genetic distances in the Buryats, the assumption of linearity appears to be violated. This conclusion is based on the observation that some nonlinear transformations (i.e., logarithm, square root, and negative reciprocal) of the geographic distance have shown an improved fit in the regression and correlation.

According to Sokal and Rohlf (1981), it is appropriate in this case to use a rank-order correlation. Relethford (1990) states that the expected relationship between geography and genetics is nonlinear and that the Mantel test can be used with a rank-order correlation. Following these recommendations, we have ranked the variates (i.e., the elements of geographic and genetic distance matrices) and computed a rank-order correlation. The resultant rank-order correlation of $r_s = 0.50$ is appreciable, and this relationship is significant ($p = 0.03$). Hence it appears that a nonlinear relationship exists between geographic and genetic distances among the Buryat population subdivisions. The most likely explanation of this nonlinear relationship is that geographic barriers, such as lakes, mountains, and rivers, interfere with linear migration into the subdivisions. In addition, cultural factors such as ethnicity and nationality may contribute to the patterns of migration and gene flow.

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